VI. *Notes on the Coloration and Development of* Insects.

By P. Cameron.

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I. On the Markings on the Larvæ of *Smerinthus*.

Last autumn I made an observation which may possibly throw some light on the use of the reddish-brown marks along the sides of the larvæ of *Smerinthus*. My attention was attracted to a small poplar (*Populus nigra*) whose leaves were very much affected with the small dark blotches caused by the fungus *Melampsora populina*, Lev. When examining these, I noticed that some of the blotches appeared to be of a brighter and redder tint. On pulling a leaf down which bore these differently-coloured markings, I found, somewhat to my astonishment, that they were not fungi, but the markings along the sides of a caterpillar of *S. populi*, which I had not observed before. The question then occurred to me : Might not the markings on the caterpillar have been acquired in imitation of the fungi, so as to give it an additional means of protection, in conjunction with the green colour of its body, in imitation of the green colour of the leaf ? To test this, the caterpillar was put back again on the tree, and the effect noticed. No doubt, looking at it close at hand, the larva was readily seen, for besides the slight difference in the colour of the lateral marks and the fungi (as already explained), the colour of the body was much brighter than the leaves, which were then (the end of September) beginning to fade ; but, looked at from a distance of several feet, the caterpillar was certainly very difficult to see, and undoubtedly it seemed to me that the similarity of the spots to the fungi added not a little to hide it. Several other caterpillars were found on neighbouring trees (likewise infested with fungi), and the examination of these served to confirm my first impression of the usefulness of the marks in hiding the larva in the circumstances in which it lived. The markings on the three species of *Smerinthus* are variable, and may be entirely absent. Mr. Boscher, for instance (*Proc. Ent. Soc.*, p. xliv., 1878), describes two forms of

the larva of *S. ocellatus*—one feeding on *Salix triandra*, without markings, and another on *Salix viminalis*, with a double row along the side. We can scarcely suppose that the marks serve no useful purpose; and we have in the case of *Deilephila Hippophaes* a very good illustration of similar marks simulating objects—the berries—found on the food-plant. There is another circumstance which favours my view, the circumstance, namely, that the three principal food-plants of our species of *Smerinthus*—*Tilia*, poplars, and willows—are much infested on the leaves with fungi (as the poplar), or, as with all three, with mites (*Phytopus*), which form on the leaves little galls of from 1 to 3 ″ in length, and usually of a brownish-red colour; while they are, like the fungi, very common, and have a wide distribution. On a willow (*Salix aurita*) close to where I discovered the caterpillars, I found many mite-galls on its leaves, and compared them with the markings in the caterpillar. Many were larger, and many smaller, while the colour was scarcely so bright in most cases, but still at a distance of a yard or two the resemblance was considerable, and could only be detected by a practised eye. I do not know if the spotted caterpillars are found only on infested trees, or the contrary; what I contend for is, that these and similar excrescences, being so common on the food-plants (and indeed on most plants near those frequented by the larvæ), the reddish markings serve to protect them.

In the above-mentioned caterpillar of *S. populi*, the red spots were fully larger than those in Weismann's figure of *Deilephila Hippophaes*,* and they were the same in number (6); the spiracles too were surrounded with red; but these red blotches, though more numerous, were scarcely so large as those on the upper row, although conspicuous enough.

My observations have shown too, I think, that they do aid in concealing the larva on an infested tree. The fact of the spots appearing late in life may be owing to the caterpillar's increased size rendering it more conspicuous than it was when younger, and, consequently, standing more in need of additional means to aid concealment. It may be added that *Hippophae rhamnoides*, the food-plant of *Deilephil a Hippophaes*, has a *Phytopus*† attached to it;

* Descendenz—Theorie, ii., pl. iv., f. 59.

† cf. Rudow. *Pflanzen-gallen Norddeutschlands*, p. 173.

and if its galls be like those on willows, &c., they would have, at least, a general resemblance to the reddish markings on the caterpillar, and the similarity between the two may serve to hide the caterpillar when the berries are unripe or absent, or even when they are present.

II. Further Notes on the Coloration of Saw-Fly Larvæ. *

a. On the Changes of Colour undergone by certain Larvæ. —It has long been known, from the observations of Reaumur, De Geer, and many modern observers, that many saw-fly larvæ, immediately before pupating, change colour, becoming, as a rule, more obscurely and uniformly coloured, and throwing off any hairs, spines, &c., which they may have carried before. What is the meaning of this change? It might be said that in the case of a spiny larva it was in order to give it greater freedom to spin the cocoon, but obviously this answer will not explain why spineless larvæ change. The change of coloration is most conspicuous with gaudily-coloured larvæ, as, for instance, with the gooseberry grub, whose two forms of larva are often taken for two distinct species. All gaudily-coloured larvæ do not change colour; while, on the other hand, others, whose coloration is obscure, do so, although in this case the difference between the two is not very conspicuous. Unfortunately, our knowledge of the habits of these creatures in a state of nature is still somewhat limited, especially as to their modes of pupation. We cannot suppose that the change is altogether useless and meaningless, and I believe further observation will show that it is protective, either in concealing the creature, or by making it more conspicuous in the case of noxious larvæ. Saw-fly larvæ are seldom large; protected larvæ therefore can only make their presence known by feeding in company on a leaf; but when they become full-fed they have to separate, to descend to the earth to seek a resting-place, and while doing so they encounter new enemies, and are exposed to dangers of a different kind from what they had been accustomed to. Hence a change of colour might be of advantage; either a colour which would simulate the surroundings, or one which would make them more conspicuous than they were when living in companies. While some of these creatures bury themselves immediately

* See Trans. Ent. Soc., 1878, p. 141.

beneath the food-plants, others travel some distances, in order to find a suitable resting-place. This is especially the case with those which do not pupate in the earth, but bore into the stems of pithy plants, in lieu of spinning a cocoon, or because the cocoon itself is thin. Some of these species (*Emphytus, Taxonus*) I have found at considerable distances from their food-plants in stems ; and I have found a cocoon of *Lophyrus pini* in a crevice of a wall many yards' distance from any pine. The view that the change of coloration is protective is confirmed by observations I have made on two very different species, and the observations are especially interesting, as they illustrate the two forms of protective coloration. While in most cases the change is (as already mentioned) in the direction of a more obscure (generally green) coloration, in one or two instances the opposite is the case. There is a gall-making *Nematus* found abundantly along the banks of rivers on *Salix purpurea*. Living, as the creature does, in its larval state concealed in galls, it has no need of bright colours, and accordingly its body is white. At the last moult, however, it becomes entirely slate-coloured, and leaves the galls for the ground. I once found several of these larvæ on the sands which surrounded the trees, marching up to a higher portion of the river bank. I noticed especially that the colour of their bodies harmonised admirably with the sand, and thus they were very difficult to see ; certainly a white larva would be much easier detected. Another species of the same group is found on *Salix aurita*. In this case, of course, the comparison with the sand does not hold, but then the slate colour agrees quite as well with the dead grass, &c., found in the marshy situations where the species lives. The other observation relates to *Cladius viminalis*. Three or four of its larvæ feed, ranged in a row, on the underside of a poplar leaf, of which they eat only the epidermis. When very young they are entirely green; gradually orange makes its appearance on the first and last segments, black marks appear on the body, which is also covered with hair ; but still the green largely predominates. Then at the last moult every trace of green disappears, and the entire body is orange, save the black head and the black marks. The brilliant colour acquired when it has stopped feeding and is ready for pupating is explainable, I think, by a reference to the habits of the creature. Living several on a leaf, their presence is made sufficiently visible during the greater part of their life ; but when they have

become full-fed they separate, and each seeks a suitable hiding-place. They do not pupate apparently on their natal tree, but descend it to go in search of another, up whose trunk they march, and spin their cocoons in crevices. I have found them doing this on trees—firs, beeches—many yards' distance from any poplars. Last September I found one far from the food-plant, about six feet up on the trunk of a beech, where it was readily noticed by its gaudy colour. It was put into a tube, and in half an hour had begun to spin its cocoon. Here, then, we have the reason for the gaudy coloration acquired at the last moult; it is to make it more conspicuous than it would be if it had retained the green which it had when feeding. The species of this genus spin an irregular, thin, semi-transparent cocoon, which is spun either in chinks in the bark, or in stems of herbaceous plants. Hence they may have to go some distance before a proper place is met with.

b. Dimorphic larvæ.—The question of dimorphic larvæ with the *Tenthredinidæ* is one well worthy of attention. The subject is at present somewhat obscure, for although I have bred forms, which I cannot separate in the perfect state from differently-coloured larvæ, and might therefore conclude that they were dimorphic larvæ of the same species, yet further observation might show that in reality they were distinct species. I am not now referring to such cases as *Lophyrus similis* and *L. pini*, and *Nematus cadderensis*, Cam. and *N. croceus*, Fall. (*fulvus* II.); for although in these two cases the perfect insects cannot be separated by any distinct characters, yet the larvæ are so different in form, coloration, and habits, as to preclude the idea of their being dimorphic larvæ of the same species. I am alluding to such forms as I have described elsewhere,* where larvæ differently marked (but still having some common characteristics) produced imagos which cannot —or, at any rate, I cannot, nor can Herrn Brischke and Zaddach, as they inform me *in litt.*—be satisfactorily separated. *Nematus capreæ*, Pz., has two forms of larvæ: one, the common type, green, with white lines; and a much rarer form, which is reddish, but with the same markings as the other. Both feed on the same food-plant (*Carices*) and in the same locality. One or two species of *Cimbex* would appear

* *Fauna of Scot.*, p. 41.

to have dimorphic larvæ, but the specific distinctions between the forms of this genus are yet too complicated to enable us to decide if the different larvæ belong to the same or to different species. Brischke and Zaddach* (and no better authorities could be stated) describe two distinct forms of the larvæ of *Cimbex saliceti*, Zad. (*lutea* auct.) on *Salix caprea*—one brownish-red, and a rarer bluish-green one. The larva of another species of *Nematus* (*histrio* Lep.), is in the great majority of cases green, but specimens are occasionally of a decided reddish hue, although I have never seen the red predominating to such an extent as with the red form of *N. capreæ*.

I find that the larvæ of the various species of *Cimbex* and *Trichiosoma* are not at all clearly defined, any more than are the perfect insects. Dahlbom † had an idea that the great variability of the imagos was produced by the food-plants, but this I regard as very doubtful; and it is certain that some forms which Dahlbom regarded as varieties are good species, presenting distinctive (although slight) characters in their larval and imago states. Several varieties of *Cimbex sylvarum*, for instance, are bred from birch, and of *C. saliceti* from willow; while the form mentioned by Dahlbom from beech is considered by Brischke and Zaddach as a good species.

c. On the Use of the Hairs on Green Larvæ.—I have already alluded to the difference in the mode of feeding of the protected and edible larvæ which feed on the flat surface of the leaf. Besides this difference in habits, there is a structural peculiarity which distinguishes them. It is that the noxious larvæ have bare, shining bodies; whereas the others have their bodies more or less covered with pale hairs. With flat larvæ, as in *Camponiscus*, they are only along the edge, which is very projecting and waved, so that the legs are entirely hid. In *Nematus pallescens* the body is more cylindrical, and covered all over with pale hairs, which, although of moderate length, cannot be seen unless the larva be examined close at hand, when it is resting on the leaf. In *Cladius*, again, the bodies are still more cylindrical, and the hairs are longer. Now, hairs of this class appear to be entirely confined to larvæ (generally green) which feed on the surface of the leaf,

* Schr. ges. König. III., pl. 11, f. 4.
† Prod. Hymen. Scand, 50.

and, with scarcely an exception, to edible ones. *Cladius viminalis* has these hairs, like the other species of this genus, but they do not add in any way to its conspicuousness, for they are pale and scarcely noticeable, and therefore cannot be ranked with the hairs on the gooseberry grub (*Nematus ribesii*), which undoubtedly tend to render it more easily seen.

From the pale woolly appearance of these hairs, and from the fact that most of the larvæ of *Cladius* are green and inconspicuous, it is probable that *C. viminalis* and *C. aeneus*, Zad., are the youngest species, and that the hairs derived from the primitive pale-coloured ancestor have been retained, although no longer aiding concealment.

Now what is the use of these hairs? I believe that suggested by Meldola and Lubbock,* to prevent the body throwing a sharp shadow on the leaf, which would certainly happen if the bodies were perfectly bare. It is possible, too, that the hairs in *Cladius*, and the spines in *Blennocampa* (*e.g.*, *B. geniculata*), may in addition to this purpose, serve as a protection against the attacks of ants and other carnivorous insects. I believe the green, spiny larvæ are as a rule nocturnal feeders, resting motionless during the day on the underside of the leaf. Such, at any rate, is the habit of those of *Macrophya sturmi*,† Kl., which feed in company, and they give out a bad smell. One kind of larva of this class (*Nematus compressicornis*, Fab., *vallator*, Voll.)‡ has the curious habit of surrounding itself with a wall of dried bubbles secreted by itself, apparently as a protection against insects.

In regard to this subject, I notice a very suggestive remark by Fritz Müller,§ which is very well illustrated by certain Tenthredous larvæ. He says (alluding to the caterpillars of butterflies) that obscurely-coloured larvæ must either live solitary and hide themselves, or acquire a bad odour and congregate together. These, by living in companies, surround themselves with a fetid atmosphere, and thus make their presence as effectually known as if they were gaudily coloured, or armed with hairs and spines. This is precisely what we find with the larvæ of *Eriocampa*, and others, as mentioned in my last paper. *Eriocampa adumbrata* appears to have reached the

* Trans. Ent. Soc., 1878, 214.
† Cf. Kaltenbach, *Pflanzenfeinde*, 83.
‡ Cf. Vollenhoven, Tijd. Ent., i., 191, pl. 12.
§ Quoted Proc. Ent. Soc., 1878, vi.

highest phase of this protective coloration ; for not only do its larvæ have a bad smell, and are covered with a resinous secretion, but they resemble very closely the droppings of a bird.* *Dineura stilata* and *D. degeeri* afford other instances. I am strongly inclined to believe that the obscure coloration of these protected larvæ has been acquired as a protection against ichneumons, by rendering them less conspicuous, while the secretions have been acquired against the attacks of carnivorous insects. Flat larvæ like those of *Eriocampa* cannot defend themselves with the abdomen like those which feed along the edge of the leaf, as I have already explained. It is worthy of remark that the *Eriocampa* and *Dineura* larvæ are not always exhaling the odour, but only when danger is near.

It may be noted here that the habit of congregating together on the upper or lower surface of the leaf, and eating only the epidermis, is not confined to saw-fly larvæ. We have a very good illustration of it with *Phratora vitellinæ*, the beetle whose larvæ are so common on willows. And the reason of it is obvious. A large, gaudily-coloured larva might live apart, and be still easily observed; but the only way small larvæ can make their presence known is by massing together.

III. On Parthenogenesis in the Tenthredinidæ.

The first indication of the occurrence of Parthenogenesis with the *Tenthredinidæ*, was recorded by a gardener named Thorn,† who had observed *Nematus ribesii* to deposit fertile eggs without having had any access to males. This observation remained unverified until 1866, when Kessler, a German naturalist, confirmed it.‡ The same species formed the subject of many careful and extended experiments by Von Siebold§—experiments which proved beyond all doubt that Parthenogenesis was a common phenomenon with this saw-fly ; and that only males were produced out of the unfertilised eggs.

Last year I experimented with *N. ribesii*, and had no difficulty in getting several females to lay eggs without

* As remarked by Jordan, Ent. M. Mag., viii., 252.

† *Gardener's Magazine*, vii., 196.

‡ Die Lebensgeschichte von Ceutorhynchus sulcicollis und Nematus ventricosus. Cassel, 1866.

§ Beitr. zur Parthenogenesis der Arthropoden. Leipzig, 1871, pp. 106—130.

their having had any connection with males, and from these eggs I bred only males. A few years ago I got an unfertilised ♀ of *Nematus miliaris*, Pz. (*viridis* Htg.), to lay eggs, but the larvæ which they yielded, unfortunately died in the cocoons during the winter.* Last year I was more successful with this species, and succeeded in rearing the imagos from unfertilised eggs: they were all males. *N. miliaris*, I may remark, has the males—if not as abundant as the other sex—tolerably numerous. I was also fortunate enough to get *Strongylogaster cingulatus* Fab., *Phyllotoma nemorata*, Fall., and *Hemichroa rufa*, Pz., to lay unfertilised eggs, which yielded larvæ, but unfortunately they all died very young. The ♂ of *S. cingulatus* is known, but is certainly very rare; while the males of the other two are quite unknown, although they are very common species and have been often bred. I experimented with several other species, but the result was altogether negative: they would not lay; nor indeed would all the individuals I had of the species I have mentioned.

Mr. J. E. Fletcher, of Worcester, has kindly communicated to me the results of some experiments he made last year on the same subject.† He got the common gall-making species, *Nematus gallicola (Vallisneri)* to oviposit, but the gall did not come to maturity, owing apparently to the plant being small and weak. Mr. Fletcher was more fortunate with *Nematus curtispina*, Thoms., and *N. palliatus*, Thoms., having managed to rear from unfertilised eggs 21 ♂ and 1 ♀ from the former, and 2 ♂ from the latter species. That a ♀ should appear as with *N. curtispina* is certainly very exceptional, but I have no doubt of the correctness of Mr. Fletcher's observations; although it is quite possible that the egg may have been brought in with the food-plant, or a pupa may have been put in by mistake, as happened to Von Siebold when conducting his experiments. Both species are closely related to *N. miliaris*, but both are good species.

From the above remarks it will be observed that the experiments were only completely successful with those species which have the males tolerably common; while they have only shown that those species which have the males exceptionally rare, or altogether unknown, are capable of laying fertile eggs, but without telling us if they

* *Scot. Nat.*, iv., 157.

† See also Ent. M. Mag., May, 1880, p. 269.

would yield males or females. The unfertilised eggs of *S. cingulatus* might produce males; but the probability is that *Hemichroa rufa* and *Phyllotoma nemorata* would give issue to females, seeing that no one has ever caught or bred the males of these common species. There is equally good evidence that complete parthenogenesis occur with *Eriocampa ovata*, L., and *Poecilosoma pulveratum*, Fall. (*obesum* Klug.). The late Frederick Smith once bred between 300 or 400 flies from the larvæ of *E. ovata*, and not one of them was a male, while it has recently been shown by Mr. Bridgman* that an unfertilised female can lay fertile eggs, but Mr. Bridgman's larvæ unfortunately died young. I have shown too elsewhere † that *P. pulveratum* (whose male is unknown) is a parthenogenetic species. I think then we are justified in concluding that complete and mixed parthenogenesis exist in the *Tenthredinidæ*.

Von Siebold in his book has analysed Hartig's *Blattwespen* in reference to the scarcity of males with these insects, and shows that Hartig was apparently unacquainted with the males of 76 species out of a total of 381. Since the publication of Hartig's classical work, our knowledge of the habits of saw-flies has enormously increased, while the differences between the sexes are much better understood. Still, with all that, the males of many species remain to be discovered. I find that out of some 330 British species, the males of 53 have yet to be found. No doubt many of these are rare and little known forms, so that much stress cannot be laid on them as showing the scarcity of males, but the same result is shown in another way. Tabulating the British species in my collection, I find that, in addition to the maleless species noted above, 54 species are represented by females only, so that altogether I have never seen the males of 107 species. In the large genus *Nematus*, the males are very much rarer than the other sex, even with common species. *Nematus pavidus*, ‡ for example, is a species I breed regu-

* Ent., 1878, 191.

† Ent. M. Mag., xv., 12.

‡ Last autumn I found about two dozen of the larvæ of this species on a willow bush, nearly full-fed. They were placed in a jar together with not more than a day's supply of food, and forgotten for a week. Most of them were then found dead: two spun cocoons and yielded ichneumons (*Mesoleius opticus*), and three had turned to pupæ without spinning a cocoon. These proved to be two males and one female, the former of the usual size, the latter rather small and dark coloured.

larly, yet I have only got four males during several years. Now males are, as a rule, much easier bred than females owing to their smaller size, and to their appearing seven or eight days earlier than the females, so that, if they were at all common, the chances are all in favour of the observer rearing them.

The phenomenon would appear to occur with closely allied species in all the genera. Thus we have (mentioning only common species) *Hemichroa rufa* with the ♂ unknown, and *H. alni* with it very rare, while the closely allied *Dineura verna* has no male. Then there are *Poecilosoma pulveratum* and *P. luteolum*, and two or three species of *Fenusa* with no known males; the same is the case with *Blennocampa albipes* and *B. ephippium*, while the closely allied *B. fuscipennis*, Fall. (*luteiventris* Kl.), has the ♂ very rare. So it is with the too common *Eriocampa adumbrata*, while, as stated already, *E. ovata* is unisexual. Again, the males of *Hoplocampa brevis*, Kl., and *H. rutilicornis*, Kl., have not been described, while of the large genus *Nematus* we have *N. Erichsoni*, Htg., and *pallidiventris*; *leucotrochus*, H., and *conductus*, Ruthe; and (as before mentioned) *palliatus*, *curtispina* and *miliaris*.

Note.—Since writing the above paper, Mr. Meldola has directed my attention to a paper of his (Proc. Zool. Soc., 1873, p. 155) wherein he has given a similar explanation of the change of coloration in larvæ before pupation to that stated on p. 71. Mr. Meldola gives as examples of this habit various species of *Lepidoptera*.